PREDATION ON RED-WINGED BLACKBIRD EGGS AND NESTLINGS

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The contents of Red-winged Blackbird (*Agelaius phoeniceus*) nests are subject to extensive and highly variable losses. Normally, most red-wing eggs fail to produce young that are able to leave the nest. Most researchers have found 60 to 100% of the losses to be due to predation on nest contents, where the entire brood or clutch is lost at once. Fewer than 5% of the losses normally appear to be related to starvation of nestlings or nestling competition. The remainder of the losses (under 40%) result from a variety of causes including egg infertility, nest desertion, and nest tipping due to growth of the supporting vegetation. In this study, I relate predatory losses of red-wing nestlings and eggs to water depth at nest-sites, habitat type, and number of young in the nest. My studies were done in east-central Kansas: several previous authors have presented data from similar studies in other parts of the range of the Red-winged Blackbird (Goddard and Board 1967; Robertson 1972, 1973; Case and Hewitt 1963).

METHODS AND STUDY AREAS

Red-wings were studied at 6 areas within 20 km of Manhattan, Kansas. Two upland sites had similar topography and vegetation and were within the Konza Prairie Research Natural Area, south of Manhattan. Each consisted of a draw containing a small strcam and the surrounding lowland. Vegetation was of the tall grass prairie type, largely treeless. Red-wings nested in scattered brushy growth, primarily buckbrush (Symphoricarpos orbiculata) and willow (Salix spp.). Except for one 4 m diameter pool in area A, there was no standing water and no cattails (Typha latifolia). A third study area, north of Manhattan, was also designated "upland." It was similar to the Konza areas but contained many young trees and was bordered by farmland.

The remaining 3 areas were designated "marsh." Two of these were on the edges of an old oxbow of the Kansas River, and contained large unbroken stands of cattails and standing water up to 80 cm in depth. In 1974, water completely disappeared by early July in all but 1 corner of one of these areas. The third marsh area was a cattail marsh below the dam at Tuttle Creek Reservoir north of Manhattan.

Data were taken in all areas during the 1974 nesting season, and in the marsh areas in 1975. Red-winged Blackbird nests were located and marked with small flags placed about 10 m from the nest-site. Water depth at the nest-site at the time of discovery was measured, nest contents were noted, and Brown-headed Cowbird (*Molothrus ater*) eggs were removed when present in the nest. Nests were visited on alternate days until the clutch or brood had either suffered catastrophe, been abandoned, or the young had fledged. I include here only nests that were discovered prior to hatching and for which the subsequent history is known.

Brood sizes in most nests were experimentally manipulated by removing nestlings from

I nest and adding them to another. Nestlings were moved as soon after hatching as possible (usually the same day) and broods were augmented only by nestlings of the same age in days. Thus "augmented" broods had more young in the brood than there were eggs in the original clutch, and "depleted" broods had fewer young. "Natural" broods had the same number in the brood as were present in the original clutch, and included several nests to which nestlings were added at hatching but in which natural brood reductions occurred early in the nestling period.

When a nest was encountered that had been preyed upon since the last visit, observations were made on contents of the nest, condition of the nest, condition of the supporting vegetation, and on predator tracks when they were present. Measures of predation pressure were calculated after Mayfield (1961) as "Number of nests preyed on"/"Number of nest-days exposure" in order to account for finding nests in which eggs had been present for varying lengths of time. Chi-square analysis by Dow's method (1978) was used to determine the significance of differences between predation rates. This method accounts for the fact that the Chi-square test cannot be used on data which are not independent frequency data. Frequencies of successful and preyed-upon nests were calculated from predation pressure values based on 23 days of exposure for the average nest.

RESULTS

Based on signs left by the predators of red-wing nest contents, I categorized predation into 3 types. Type 1 was eggs or nestlings gone with the nest left intact, and was thought to be the result of avian predation, particularly by the Common Grackle (*Quiscalus quiscula*). or occasional predation by snakes, possibly the water snake (*Natrix sipedon*), which is locally common.

Type 2 predation was the nest and supporting vegetation ripped down, with the eggs or nestlings gone. It was thought to be due primarily to raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and to a lesser extent mink (*Mustela vison*). Type 2 was the most distinctive and recognizable type of predation found.

In type 3 predation, the nest was intact, the eggs destroyed, and the eggshells left in the nest. Type 3 was observable only before hatching and was thought to result primarily from small mammal predation. Type 3 may also have involved avian predation as well and is thus not entirely distinct from type 1. No predation of any type was observed actually taking place.

Predation and water depth.—Total predation on marsh red-wing nests was inversely related to water depth at the nest-site (Table 1, Fig. 1). Predation in water 0–20 cm deep was significantly greater than predation in water 20–40 cm deep ($\chi^2 = 15.6$, df = 1, P < 0.001).

The effect of water depth varied for the 3 observed types of predation. Type 2 predation, thought to be primarily raccoon, was the most intense of the 3 types, and steeply decreased with increasing water depth. Type 2 predation in water 0-20 cm deep was significantly greater ($\chi^2 = 14.1$, df = 1, P < 0.001) than type 2 predation in deeper water; in fact there were no TABLE 1

The Effect of Water Depth at Red-winged Blackbird Nest-sites on Predation Pressure ¹										
Water depth		No. nest-days	No.	nests	preyed up	pon	P	redation	ı pressur	e
(cm)	No. nests	exposure	Type 1 Type 2 Type 3 Total			Type 1	Type 2	Type 3	Total	
0-10	72	917	4	33	12	49	0.004	0.036	0.013	0.053
10-20	68	720	12	10	9	31	0.017	0.014	0.012	0.043
20-30	16	227	1	0	1	2	0.004	0.000	0.004	0.009
30-40	5	69	1	0	0	1	0.014	0.000	0.000	0.014

¹ Predation pressure = no. nests preyed upon divided by no. nest-days exposure.

recorded instances of predation by large mammals in water deeper than 20 cm. Since type 2 was the most intense component of observed predation, water depth effects on type 2 are largely responsible for the overall negative correlation between predation and water depth.

Type 3 predation, thought to result primarily from small mammals, did not significantly decline with water depth ($\chi^2 = 2.4$, df = 1, P > 0.05). Type 3 predation was significantly less intense than type 2 in water 0–10 cm deep ($\chi^2 = 12.9$, df = 1, P < 0.001) but closely corresponded to type 2 values in deeper water. Type 1 predation, thought to be avian, was also not significantly influenced by water depth ($\chi^2 = 0.1$, df = 1, P > 0.05).

The lack of nests in water deeper than 20 cm probably reflects a paucity of suitable emergent vegetation in which to nest. Because there were only 21 such nests, the differences among the predation rates for these nests were subject to relatively great random variation.

Predation in marsh and upland habitat.—Predation differences cannot be meaningfully related to habitat per se, without recognizing variables inherent in the term habitat. Thus consideration of water depth, nesting density, and other potentially important factors should be made, and only then extended to include habitat differences in predation. My data (Table 2) show no significant difference ($\chi^2 = 0.03$, df = 1, P > 0.05) between marsh and upland predation. Even when the effects of water disappearing in one of the marsh areas are accounted for by considering only predation before the area completely dried, there is no significant difference between total marsh and upland predation pressure, or between marsh and upland predation of any of the 3 types.

Predation and brood size.—Variation in water depth, season, and predator species identity, unless they are accounted for, tend to obscure effects of brood size on predation rate. To eliminate those effects, I considered only

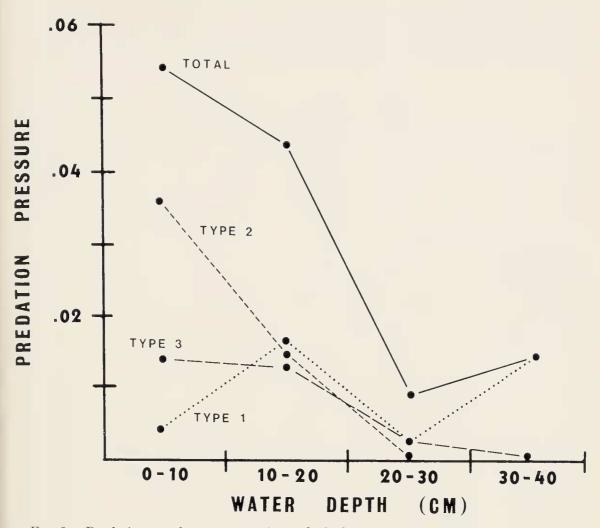


FIG. 1. Predation on the contents of marsh Red-winged Blackbird nests, as a function of water depth at the nest-site.

nests in water less than 20 cm deep, which were relatively available to all predators. Data from the entire season were lumped together to reduce the effect of seasonal changes in the influence of brood size on predation, and predations of the different types were considered separately to account for different predator species types.

TABLE 2

Predation on Red-winged Blackbird Nest Contents in Marsh and Upland Habitat

		No.	No. nests preyed upon				Predation pressure			
Habitat type	No. nests	nest-days - exposure	Type 1	Type 2	Type 3	B Total	Type 1	Type 2	Type 3	Total
Marsh	161	1933	18	43	22	83	0.009	0.022	0.011	0.043
Upland	33	383	7	6	2	15	0.018	0.016	0.005	0.039

	No. nests (water depth	No, nest-days exposure (after	No. nests 1	preyed upon	Predation pressure	
	$at site \leq 20 cm$)	(after hatch)	Type 1	Type 2	Type 1	Type 2
Brood size: 2	24	180	4	3	0.022	0.017
3	21	142	2	4	0.014	0.028
4	9	64	1	2	0.016	0.031
5	22	165	2	6	0.012	0.036
Brood manipulation	category:					
Augmented	25	189	2	7	0.011	0.037
Natural	15	95	2	2	0.021	0.021
Depleted	44	332	8	8	0.024	0.024

The Effect of Brood Size and Brood Size Manipulation on Predation Pressure

TABLE 3

Table 3 relates after-hatch predation pressure of types 1 and 2 to the number of nestlings present in the brood and to brood size manipulation. Augmented, depleted, and natural broods are lumped in the "brood size" data. Type 1 predation was negatively, but nonsignificantly correlated with brood size (r = -0.84, P > 0.05), while type 2 predation was positively and significantly correlated with brood size (r = 0.96, P < 0.05). The actual number of young present in the nest may not have been as important in influencing predation as artificial manipulation of the number present, but larger sample sizes are needed to determine whether this is so.

DISCUSSION

Water depth at nest-sites was significant in its effect on predation pressure, and the effects were predator-specific. Mammalian predators were deterred increasingly with increasing water depth beneath nests while avian predators were not apparently influenced by the presence of water. Diminishing returns associated with deep-water foraging may correspond to the depth at which mammalian predators must begin to swim, and thus account for the sharp decrease in predation at a depth of approximately 25 cm. My findings agree with those of Robertson (1972), who found a negative correlation between percent red-wing nests preyed on and water depth, and Goddard and Board (1967) who found nesting success to increase with increasing water depth at nest-sites. Francis (1971) in a review of red-wing literature, found no significant difference in nesting success for sites of varying water depth. Because influence of water depth varies with mammalian predator species identity, because avian predation apparently occurs independently from water depth and because non-predatory nest destruction can be significant, overall nesting success will not always be well correlated with water depth. While predation is normally the most important determinant of nesting success, it is not the only one.

Red-wing nesting densities are normally higher in marsh than in upland habitat. Robertson (1973) has found nest densities that differ by as much as an order of magnitude. Thus, in marsh areas with relatively shallow water, predators should be more efficient than upland-searching predators in finding nests. Further, by temporarily specializing on marsh red-wing nest contents as they become seasonally dense, predators could maximize their prey discovery rate. This "switching" in predators (Murdoch 1969) would be enhanced if they are able to form a search image, or key on the activity of the females caring for their hatchlings. My data may reflect such density dependent switching, particularly where, with decreasing water depth, nests became available to mammals. In some cases, signs left at nests preyed upon by raccoons indicated a systematic searching pattern, resulting in nearly complete destruction of the red-wing nesting in the area.

My observations do not support Robertson's (1972, 1973) hypothesis that nesting synchrony and the tendency toward nesting coloniality in marsh sites results in high enough nesting density to satiate predators and thus reduce the probability of predation on each nest in the population. However, I have no density data and may have been dealing with nests in a positive densitydependent predation range, resembling other populations studied by Robertson. More work clearly needs to be undertaken, perhaps in manipulation of nest density.

Water depth and nest density probably constitute important variables in most habitat differences in predation on red-wing nest contents. The frequently observed pattern of higher predation in upland than in marsh sites (Robertson 1972, 1973; Francis 1971; Case and Hewitt 1963) should thus normally be explainable in these terms. The presence of water in marsh habitats may also influence the density of nests by allowing higher nesting densities without corresponding high predation rates. Further, benefits which accrue from the "mobbing" of potential nest predators, a behavioral consequence of the density itself rather than a habitat factor, may make dense nesting even more reproductively advantageous.

My observations indicate that some aspect of brood size or experimental manipulation of brood size affects predation rate. Unfortunately, my sample was not large enough to determine which of these is more important. If clutch-size is adapted to the limits of the female's feeding ability (Lack 1954), adding a nestling could result in a disruptive change in the feeding activity of the female. Brood activity might also be increased due to increased nestling hunger, and in the presence of predators keying on activity at the nest, augmented nests would be subject to increased predation rates. Natural differences in brood size, however, could result in increased feeding activity by the female or increased brood activity, producing the same effect. Since nocturnal predation constituted more than half of the predation I observed, brood activity may have been what attracted predators.

SUMMARY

Predation pressure on the eggs and nestlings of Red-winged Blackbirds was related to water depth at nest-sites, habitat type, and number of young in the nest. On the basis of signs left by predators, predations were classified into 3 types, thought to correspond to avian, large mammal (primarily raccoon), and small mammal predators. Mammalian predation was greater for shallow water nests than for deep water nests, particularly for large mammalian predators, the most important predator type. Avian predation was not significantly influenced by water depth. Total predation on nest contents was not significantly different between marsh and upland situations. Mammalian predation increased with brood size, where some broods were of artificially manipulated size. This pattern may or may not exist apart from experimental brood size manipulation.

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APPENDIX

Predation and season.—Using data from 1974 when both marsh and upland sites were studied, predation pressure was calculated for 5-day intervals over the season (Table 4). Because the maximum number of nests extant during any 5-day period during 1974 was only 20, predation rates varied widely with small differences in the number of nests

TABLE 4The Effect of Date on Predation Pressure, 1974										
	No. nests extant		No. nest- days exposure		No. nests preyed upon		Predation pressure			
Date	Marsh	Upland	Marsh	Upland	Marsh	Upland	Marsh	Upland		
June 10-15	12	15	45	65	1	1	0.022	0.015		
15-20	17	18	62	80	4	2	0.064	0.025		
20-25	20	13	72	49	3	3	0.042	0.061		
25-30	18	13	78	54	2	3	0.026	0.055		
July 1-5	14	9	65	33	3	1	0.046	0.030		
5-10	9	5	30	24	1	0	0.033	0.000		

preyed upon. Because these data show no significant trends, they are included to allow lumping with other small samples in subsequent analysis of predation patterns by other workers.

REQUEST FOR ASSISTANCE

Mississippi Kite color-banding.—Mississippi Kites are being marked with colored leg bands and patagial tags in western Kansas and Okłahoma, and north-eentral Texas. Each kite carries a Fish and Wildlife band and from 1–3 additional color bands in combinations of red, blue, green, yellow and silver. Kites captured as adults also wear a pair of plastic patagial streamers on the dorsal surface of the wings. Streamer eolors are red, dark blue, light blue, orange, yellow, and green; about one inch of each streamer extends beyond the ends of the secondary feathers. Persons observing the marked kites are requested to send as much information about the kite and its situation as possible to: Chief, Bird Banding Office, Office of Migratory Bird Management, Laurel, Maryland 20811. Please send a copy, plus any additional information, to the bander, James W. Parker, Biology Department, State University College, Fredonia, New York 14063.